appear to be an indicator of the presence of environmental stress, and more particularly of the precise beginning and end of the period over which the stress operates. The present difficulties of the Rottnest quokka are believed to be due to recent human-related changes in the vegetation (mostly by burning and overgrazing) which have altered the vegetation from a dense woodland and shrubland to an open steppe dominated by species less palatable to the quokka and annual weeds (Storr 1963, Pen and Green, this volume). However the results of a study of quokkas living on Bald Island (Hart 1980) suggest that the Rottnest quokka may already have suffered a severe summer starvation before European settlement. Before this time only native serotypes could have been involved in the annual proliferation.

At present the annual proliferation of *Salmonella* in the Rottnest quokka represents a significant reservoir of infection and this situation results from the degraded environment afforded the Rottnest quokka. The annual proliferation will go on until seasonal starvation is removed as the dominant feature of the biology of the Rottnest quokka. The feeding experiment described by Hart (1980) suggests that this could be achieved, by restoring the vegetation and controlling the population so that suitable forage was available. A more difficult problem is the transfer of serotypes between Rottnest and the mainland. New introduced serotypes on Rottnest can only exacerbate the problems, while the transfer of *S. javiana* to the mainland could have serious consequences (see Iveson and Bradshaw 1973).

Hart (1980) has discussed the more general application of *Salmonella* infections as indicators of environmental stress on wild animals. He has proposed that while any large concentration of *salmonella* suggests such stress, the presence of introduced serotypes indicates either heavy input from another source (as has been described by Iveson 1979, for Carnac Island by silver gulls) or that the host has been rendered susceptible to infection and has amplified a small input (as has happened on Rottnest Island and particularly Bald Island). These ideas may find application in the management of natural ecosystems.

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Botanical exploration and vegetational changes on Rottnest Island

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Abstract

The former, extensive cover of low closed forest and closed scrub, characterised by *Callitris preissii, Melaleuca lanceolata* and species of *Acacia*, has declined in area from perhaps 1 000 ha in 1919 to less than 150 ha today, and has largely been replaced by low shrubland dominated by *Acanthocarpus preissii*. These changes, which have not been quantitatively documented, appear to be related to wood-cutting, fire, coastal erosion and grazing by the native marsupial *Setonix brachyurus* (quokka). There is fossil evidence of the prehistoric occurrence of *Eucalyptus gomphocephala* (tuart) woodland.

Brief history of botanical investigation

The first opportunity for a scientific examination of the vegetation of Rottnest Island came in the early nineteenth century when, on 14 January 1822, a party including the botanist Allan Cunningham, from the brig Bathurst under the command of Lieut. P. P. King, landed at Thomson Bay. Cunningham made a detailed description of the flora he saw but, as he visited only the Thomson Bay area for a few hours, his observations on abundance need to be interpreted carefully (Marchant 1977).

In 1838 Ludwig Preiss, a Prussian botanist, arrived in Western Australia to collect natural history specimens apparently with the financial support of the Russian and Prussian governments. His extensive biological collections, made over a period of about three years, from December 1838, included 58 plant species belonging to 36 families, collected from Rottnest Island; these are recorded in Lehmann's "Plantae Preissianae" (Hamburg, 1844-1848).

After Preiss's visit a period of more than a hundred years passed before any further scientific work on the vegetation of Rottnest Island was undertaken. Somerville (1949) touched only briefly on the natural vegetation of the island, being mainly concerned with the planting of exotic species. In 1952 W. M. McArthur, in studying the plant ecology of the coastal islands near Fremantle, examined the plant communities of Rottnest Island in some detail (McArthur 1957.) In dividing the vegetation into four associations and three communities, McArthur's was the first attempt at a formal vegetation classification: it was to stand for some 17 years, later classifications differing from it mainly in the further subdivision of the littoral and succulent communities. McArthur's classification is compared with others in Table 1. He included in his publication a list of 75 native and 21 introduced plant species.

An extensive fire on the island, in February 1955, provided the stimulus for the first detailed botanical study of Rottnest Island. A study of the flora and vegetation of the island was carried out in 1955 and 1956 by R. D. Royce and J. W. Green of the State Herbarium. They made extensive plant collections, monitored post-fire regeneration, set up sampling plots and transects, and compiled a vegetation map. After a time they were joined by G. M. Storr whose interest in the vegetation began in relation to the diet of the quokka, and D. M. Churchill who had discovered plant microfossils and macrofossils in the lake sediments.

A simplified description of the vegetation was given by Storr, Green and Churchill (1959) who made no attempt at a formal classification but recognized five elements in the present vegetation: supralittoral, coastal dune, interdunal, limestone ridge and swamp including salt-lake vegetation. An important finding having a bearing on vegetation changes was reported in that paper: fossil evidence was found indicating the occurrence on Rottnest Island, in Pleistocene times, of a woodland community of *Eucalyptus gomphocephala* (tuart), similar in species composition to present occurrences on the mainland. An annotated checklist of plant species was published by Storr (1962), consisting of 118 native and 62 introduced plant species. Storr's thesis (Storr 1957) also led to a further article dealing with vegetation change (Storr 1963). Besides the above publications, some information from the 1955-1956 study has been preserved in the archives of the Western Australian Herbarium, including a species list, a general account of the vegetation communities and a map showing the distribution of the associations, consociations and other communities then recognised.

In 1974 B. J. White and R. J. Edmiston of the Western Australian Forests Department reported an investigation aimed at prescribing a management programme for the maintenance and rehabilitation of the island's vegetation. Their report contained a classification of the vegetation into 9 associations and two communities, with descriptive notes on each, while in an appendix was a map taken from 1941 aerial photographs showing the distribution of low closed and low open forest (*Melaleuca lanceolata* and *Acacia rostellifera*), which they estimated as covering 400 ha.

Table 1

Plant Communities of Rottnest Island as recognized in published and unpublished reports

Name of Association (a), Consociation (ca), Community (c) or Vegetation (v)	Royce & Green (1956, unpub.)	McArthur (1957)	White & Edmiston (1974, unpub.)	O'Connor *et al.* (1977)
Olearia—Westringia (= Littoral or mobile dune)	a	v	a	c
Westringia—Acacia littorea—Scaevola (= Stable dune low dense heath)	a	..	a	c
Acanthocarpus—Stipa flavescens	a	c	a	c
Stipa flavescens	ca		....	....
Acacia littorea	a	a	a	c
Acacia rostellifera	a	a	a	c
Melaleuca lanceolata	a	a	a	c
Melaleuca lanceolata—Acacia rostellifera			a	....
Templetonia retusa	ca	a	a	c
Templetonia—Pittosporum	c	.	.	....
Pittosporum phillyraeoides	ca	. .	.	.
Sclerostegia arbuscula (= Halophytic, salt marsh)	a	c	c	c
Carpobrotus aequilaterus—Mesembryanthum crystallinum (= Mixed succulent mat)	a		a	c
Nitraria billardieri			a	c
Lavatera plebeia				c
Gahnia trifida	a	..		
Callitris preissii	a	....	.	.

More recently O'Connor *et al.* (1977) studied the vegetation and flora as part of a National Estate survey of Rottnest Island. Here the methods included quadrats, estimates of area and cover for each plant community, and the compilation of an inventory of both observed and previously-known plant species. Their species list, though based largely on Storr (1962), contained a number of new records, bringing the known flora for the island to 122 native and 57 introduced species.

Vegetation change

Early observations

Seven thousand years ago Rottnest Island probably supported a *Eucalyptus gomphocephala* woodland (Churchill 1959). This had become extinct by the time the first written accounts of the vegetation were made in the mid-seventeenth century. The first, by Volkersen who visited the island in 1658 (Appleyard and Manford 1979), noted the presence of numerous woods and thickets, as did Freycinet in 1801 and Cunningham in 1822. The latter author was particularly struck by *Callitris*, which he said "is found abundantly over the island" and, later, was "covering the surface of the island" to the point of monotony, except where "occasionally relieved by . . . melaleuca . . . and the more elegant pittosporum". Though these accounts have sometimes been taken to indicate a dense cover of trees or tall shrubs over the whole island, this was not the impression given by Wilson (1835), referred to by Marchant and Abbott (1981), who spoke about hummocks and sandhills devoid of vegetation. Wilson was probably describing the western part of the island, whereas the earlier visitors had probably seen only the environs of the anchorage in the north-east.

Settlement to 1930

Permanent settlement began on Rottnest in 1838 with the establishment of a prison. In order for the community to become self-supporting, forest was cleared to make way for farmland, roads and building sites. In addition cypress pine was felled to provide timber for construction purposes. Pigs, sheep, horses and cattle were introduced. All this activity afforded an excellent opportunity for many exotic plant species to become established on the island. The spread of these palatable plants may have caused quokka populations to increase, by increasing the island's food reserves, particularly in winter.

A dramatic change in the vegetation then began with the advent of a greater frequency of fire caused by man. Aboriginal prisoners were allowed to hunt quokkas for food; to make this easier they used their traditional method of firing the vegetation. Similarly European settlers, when hunting quokkas, deliberately lit fires to disclose their prey (Somerville 1949). Accidental fires further increased fire frequency. Both *Callitris preissii* and *Melaleuca lanceolata* are relatively fire-sensitive, regenerating after fire from seed only (Storr 1963).

It is easy to understand how a devastating fire, followed by others at close intervals, could have destroyed seedlings and depleted the soil seed bank, leading to the elimination of fire-sensitive species over much of the island. *Acacia rostellifera*, on the other hand, which is relatively fire-tolerant, owing to its ability to produce numerous suckers after burning (Marchant 1977), formed dense thickets in place of *Callitris* and *Melaleuca*. Though *Acacia rostellifera* is a very palatable plant, and thus vulnerable to quokka damage, continued hunting is thought to have kept the quokka population too low to prevent regeneration of *Acacia* (White and Edmiston 1974).

By the early 1900s *Acacia* scrub was the predominant plant community in the east of Rottnest Island, having replaced *Callitris preissii* and *Melaleuca lanceolata* in all but a few areas. R. E. Weir, a stock inspector, quoted by Storr (1963), estimated that in 1919 *Acacia* scrub covered two thirds of the island. Similarly, Glauert (1929) noted that: "much of the island is clothed with dense wattle scrub tangled with creepers and undergrowth".

1930s to the present

The success of *Acacia rostellifera* on Rottnest Island was short-lived. By the late 1930s the almost-continuous scrub began to fragment into scattered thickets. Storr (1963) believed this to be caused by the interaction of fire and quokka grazing. In the late 1920s quokkas were protected, leading in the early 1930s to a sudden increase in their numbers. No longer was *Acacia rostellifera* regeneration to proceed relatively unhampered. The species had now to contend with heavy quokka grazing, which probably resulted in the observed sharp decline in the distribution of *Acacia* scrub over the coming decades. An estimate of the rate of decline of *Acacia rostellifera* between 1919 and 1941 may be made by assuming that Weir's estimate of two thirds *Acacia* scrub is equivalent to some 1 000 ha: by 1941, judging from contemporary air photos, the total area of forest or scrub of any kind was only 400 ha (White and Edmiston 1974, see also Figure 1). This represents a decline of some 600 ha over 22 years or about 27 ha per annum.

In February 1955, fire devastated about 730 ha in the central western part of the island (Storr 1963). To investigate the effect of quokka grazing on regeneration, exclosures were erected and they and neighbouring areas were visited frequently throughout 1955 and 1956. The exercise confirmed a decline in the palatable *Acacia rostellifera* community and a corresponding increase in the less palatable *Acanthocarpus-Stipa* low dense heath in areas prone to heavy quokka grazing (Storr 1957).

The extent of forest and scrub communities was about 320 ha in 1956, ascertained from an unpublished vegetation map compiled in 1956 and preserved in the Western Australian Herbarium (redrawn in simplified form in Figure 2). These communities have continued to become reduced, largely in favour of *Acanthocarpus-Stipa* low dense heath. Since 1956 the area of *Melaleuca lanceolata* has been greatly reduced, mostly in the central areas of the island; today it is mainly restricted to the eastern end, Parker Point, and areas surrounding the lakes. Furthermore there is evidence that *Acacia rostellifera* thickets are not long-lived on Rottnest Island (White and Edmiston 1974). A stand located 60 metres south of Lake Vincent, which was seen in 1976 aerial photographs to have had a full canopy, was observed by one of us (L.J.P.) to be almost entirely dead in October 1982.

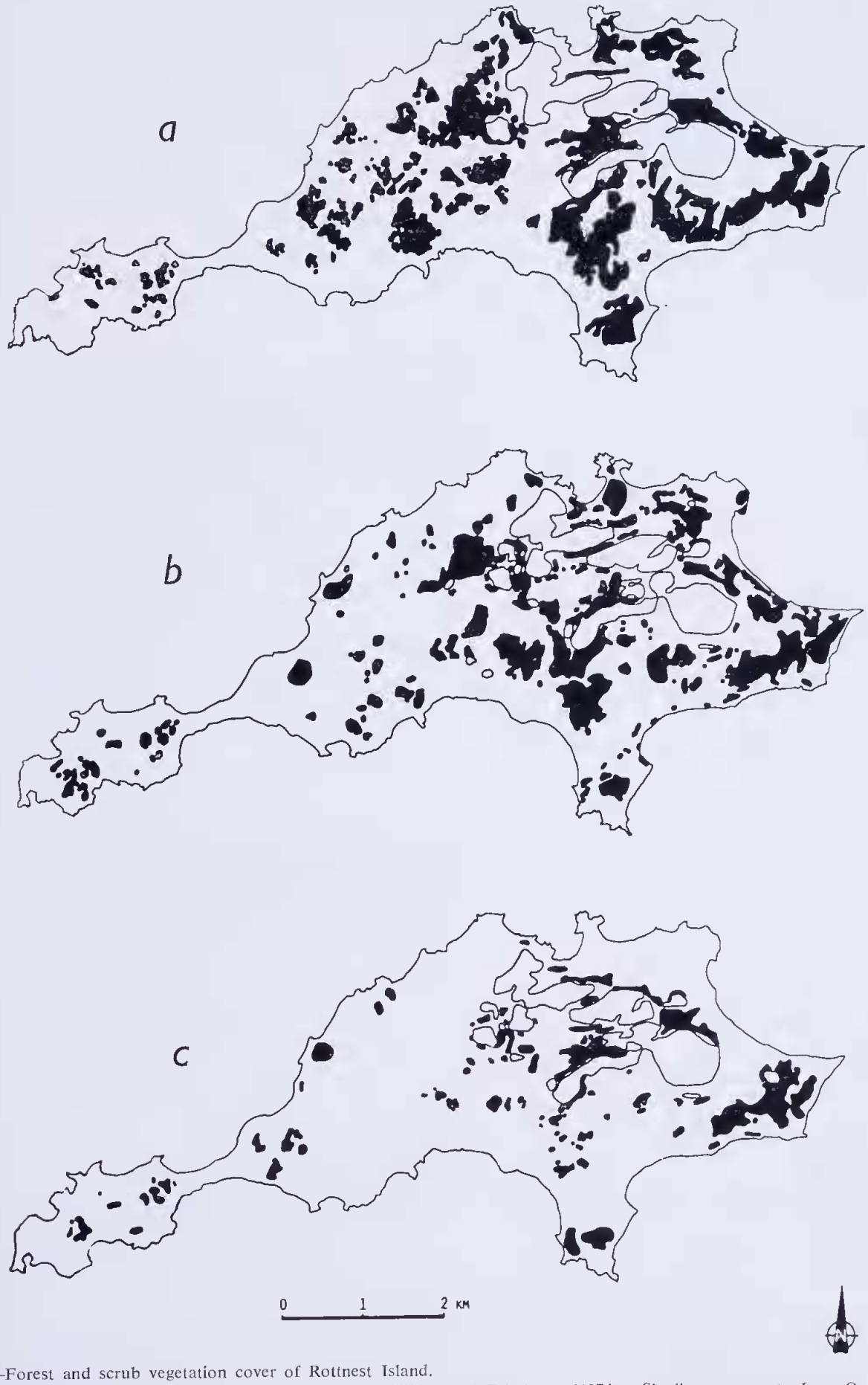

Figure 1.—Forest and scrub vegetation cover of Rottnest Island.

a. Interpretation of 1941 aerial photographs, after White and Edmiston (1974). Shading represents Low Open Forest and Low Closed Forest or Scrub communities, both comprising chiefly *Acacia rostellifera* or *Melaleuca lanceolata* as dominants.

b. From an unpublished map prepared by R. D. Royce and J. W. Green in 1956, based on 1955 aerial photographs and ground survey. Shading represents three associations: *Acacia rostellifera, Melaleuca lanceolata* and *Pittosporum —Templetonia.*

c. Based on current interpretation of 1978 aerial photographs and 1982 ground survey. Shading represents the same communities as in Figure 1b.